AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 111:369–392 (2000)

Tooth Wear and Compensatory Modification of the Anterior Dentoalveolar Complex in Humans

YOUSUKE KAIFU*
Department of Anthropology, National Science Museum, Shinjuku-ku, Tokyo 169-0073, Japan

KEY WORDS lingual tipping; attrition; occlusion; edge-to-edge bite; Darwinian medicine

ABSTRACT In populations living in environments where teeth wear severely, some compensatory modification of the dentoalveolar complex is thought to occur during life whereby functional occlusion is maintained as tooth substance is lost by wear. This study investigates one aspect of this modification process: Changes in the anterior dentoalveolar complex that are accompanied with wear were examined in a series of Japanese skeletal samples. In the prehistoric Japanese hunter-gatherer population heavy wear occurs over the entire dentition. The following changes were demonstrated to have occurred in the anterior segment of the dentition accompanied by wear on the anterior teeth: The anterior teeth tip lingually with wear up to a nearly upright position to fill in interproximal spaces that would have been generated by wear, and to maintain contact relations between adjacent teeth. At the same time, the anterior surface of the maxillary alveolar process also inclines lingually to a certain extent. The amount of lingual tipping is greater in the maxillary anterior teeth than in their mandibular antagonists. It is because of this discrepancy that, with age, the horizontal component of the overlap between maxillary and mandibular anterior teeth decreases, and their bite form changes from scissor bite to edge-to-edge bite. Lesser degrees of lingual tipping of the anterior teeth were also detected in the prehistoric agriculturists and historic Japanese populations. The variation in the degree of lingual tipping observed among the samples is explained by inter-population variation in severity and pattern of tooth wear. This and other evidence suggests that mechanisms that compensate for wear in the anterior dentition may be characteristic of all living human populations, independently of the degree of wear severity endured in their environments. Am J Phys Anthropol 111:369–392, 2000.

During the past 10,000 years the agricultural revolution, urbanization, and the industrial revolution have wrought dramatic changes in our species' living environment. Some of these changes have significantly influenced the human body in various ways (e.g., Cohen and Armelagos, 1984; Cohen, 1989; Larsen, 1997; Nesse and Williams, 1998). Documentation of the impact of these changes is important in understanding modern human health and adaptive status.

One noteworthy example of environmentally induced change over time is the decrease of tooth wear severity. It is well-known that while severe tooth wear occurred ubiquitously in prehistoric populations be-

Grant sponsor: Ministry of Education, Science, Sports and Culture; Grant number: 09740651.

*Correspondence to: Department of Anthropology, National Science Museum, 3-23-1 Hyakunincho, Shinjuku-ku, Tokyo 169-0073, Japan. E-mail: kaifu@kahaku.go.jp

Received 10 May 1999; accepted 10 October 1999.

fore the agricultural revolution, the degree of wear was reduced thereafter. The diminishment of tooth wear accompanies the development of technology, processing industries, and advances in transportation, and culminates in the conditions seen in modern societies in which tooth wear is normally limited. Begg (1954) was the first author who argued comprehensively that some dentofacial compensatory modification for tooth wear and resultant loss of tooth substance occurs in populations with severe wear in order to maintain functional occlusion during an individual's life. By proposing that horizontal and vertical movement of the teeth (mesial tooth migration and continuous tooth eruption, respectively) occurred as mechanisms to maintain contact relations between the adjacent and opposing teeth when loss of tooth substance in horizontal and vertical directions occurs through wear, Begg emphasized the continuously changing nature of the dentition and occlusion in ancient populations that underwent severe tooth wear. He further argued that this continuously changing occlusion with wear, which he labeled "attritional occlusion," is the original form of occlusion in humans. Furthermore, the decrease of wear severity and the resultant collapse of attritional occlusion caused the various dental problems seen in modern societies. Proliferation of caries, periodontitis, malocclusion, and masticatory dysfunctions such as temporomandibular joint disorder caused by occlusal interference due to unworn cusps are possible consequences pointed out by Begg and later workers (Begg, 1954; Begg and Kesling, 1977; Berry and Poole, 1974, 1976; Dickson, 1979; Kirveskari, 1979; Owen, 1986). However, others are critical of some of these notions (Luke and Lucas, 1983; Corruccini, 1990, 1991). Thus, the consequences of decreased wear are not sufficiently understood.

To advance understanding we have to clarify first the actual dentofacial compensatory mechanisms for severe wear. Although there is ample documentation of mesial tooth migration and continuous tooth eruption (e.g., Murphy, 1959; Hylander, 1977; Clarke and Hirsch, 1991a), dentofacial compensatory mechanisms for wear have not been thoroughly investigated. The purpose of this study is to demonstrate one aspect of such compensatory changes in the anterior dentoalveolar complex, which have to date received relatively little attention. The foci of attention here are changes in inclination of the anterior teeth and the bite form. Literature relevant to compensatory changes in the anterior dento-facial complex are first reviewed below.

BACKGROUND

Incisor lingual tipping

Ancient populations. Selmer-Olsen (1937) noted lingual tipping of maxillary incisors with age in Norwegian Lapp and other Norwegian skulls. This change with age or attrition was later confirmed by metric or chephalometric studies of Luntström and Lysell (1953), Lysell and Fillipson (1958), and Hasund (1965) in samples from medieval Danish, Swedish, and Norwegian sources, respectively. Though Hasund (1965) detected no significant changes in inclination of the mandibular incisors with attrition, Hylander (1977) found significant lingual tipping of both the maxillary and mandibular central incisors in a chephalometric study of Indian Knoll skulls from the USA (ca 2,000–3,000 BC). The latter author also found that the degree of inclination change with wear was greater in the maxillary than in the mandibular incisors. Varrela (1990) compared medieval and contemporary Swedish samples and interpreted the differences he detected as support for Hylander's view. Most authors thought that the lingual tipping process played a role in filling up interproximal spaces that would have been generated by wear, and thereby maintained contact relations between adjacent teeth (Selmer-Olsen, 1937; Lysell, 1958; Hasund, 1965; Hylander, 1977). Selmer-Olsen (1937) and Lysell (1958) thought that unbalanced forces of the lip and tongue muscles had caused this change.

On the other hand, Fishman (1976) and Mohlin et al. (1978) did not detect clear change in the inclination of maxillary central incisors in samples of Native Americans (10th–19th centuries AD) and medieval Swedes, respectively. The mandibular central incisors did not change in the former

study while they became procumbent in the latter.

Contemporary populations. Slight lingual tipping of the maxillary incisors has been detected even in longitudinal studies of adults of contemporary populations (Behrents, 1985; Forsberg, 1979). Sarnäs and Solow (1980) detected no significant changes in a similar study, but it should be noted that their research period (between the ages of about 21 and 26 years) is considerably shorter than those in the former two (from teens to the 9th decades and between the ages of 24 and 34 years). The mandibular incisors showed no change or a slight labial tipping in these studies.

Available longitudinal data indicate that changes in the inclination of the incisors during the growth period are small and variable among the studies. With regard to the maxillary central incisors, Perera (1990) detected average labial tipping of 1.2°, whereas significant changes were not detected in the study by Björk and Palling (1955). Changes in the inclination of the mandibular central incisors during this period were not significant in the studies by Perera (1990) and Björk and Palling (1955), while Love et al. (1990) observed lingual tipping of 1.7°. Siatkowski (1974) and Humerfelt and Slagsvold (1972) reported that the inter-incisal angle increased by 4°–7.5° between the ages of 13 and 18 years, and 11 and 25 years, respectively. Björk and Palling (1955) noted a great degree of individual variation by age in change of the inclination of the central incisor.

Krogstad and Dahl (1985) compared the dentofacial morphology of modern Norwegians between a normal group with light tooth wear and a group with advanced wear caused by some pathological activities such as bruxism, and found that the maxillary central incisors of the latter were more upright than those of the former. Johansson et al. (1993) reported a similar tendency in modern Swedish subjects.

Fossil hominids and great apes. Lingual tipping of the central incisors with advance of wear or age has been observed also in apes (Walker, 1973, and Greenfield, 1977 cited from Ungar and Grine, 1991; Dean et al., 1992). Ungar and Grine (1991) demonstrated that, in a fossil sample of South African *Australopithecus robustus*, the orientation of the occlusal surface of the maxillary central incisors changes with occlusal wear from the initial incisiolingually faced condition toward a condition perpendicular to the crown long axis. They interpreted this observed change as a reflection of lingual tipping of the maxillary central incisors with wear. A similar trend was also demonstrated in a sample of Neandertals (Ungar et al., 1997).

Summary. The central incisors tip lingually with tooth wear in several ancient North European and North American populations with severe wear, though there are some exceptions. The extent of incisor lingual tipping is greater in the maxillary central incisors than in their mandibular antagonists. Many authors hypothesize that this mechanism played a role in filling up interproximal spaces that would be generated by wear to maintain contact relationships between adjacent teeth. This is in contrast to Begg's (1954) notion that mesial tooth migration had played the primary role in filling up spaces. This mechanism is also suggested to be possessed by apes and fossil hominids. A portion of data suggests that contemporary human populations also potentially share this mechanism.

Bite form

The *overbite* and *overjet* are, respectively, vertical and horizontal components of the overlap between maxillary and mandibular opposing teeth. In this study, edge-to-edge bite is defined literally as indicating a condition where the central incisors show *overbite* = 0 and *overjet* = 0, while a condition where *overbite* > 0 and *overjet* > 0 is called scissors bite. It is widely known that living human populations have undergone a transition from edge-to-edge bite to scissors bite during the last several thousand years.

The primary cause of this temporal transition of bite form has been regarded by most workers to lie in the changes in tooth wear severity (Campbell, 1925; Smith, 1934; Emslie, 1952; Begg, 1954; Moorrees, 1957;

D'Amico, 1958, 1961; Fishman, 1976; Baba and Etoh, 1989; see Brace and Mahler, 1971; and Brace, 1977 for a contrary view). Edge-to-edge bite is a universal characteristic seen among ancient populations with severe tooth wear. In addition, observations on such populations from various regions show that the scissors bite is common during the permanent dentition formation period, and edge-to-edge bite is achieved through an occlusal modification of this subadult bite form accompanied by wear (Campbell, 1925; Leigh, 1929; Smith, 1934; Begg, 1954; Moorrees, 1957; D'Amico, 1958, 1961; Hunt, 1961). These observations have been supported by recent quantitative analyses of measurement data (Hylander, 1977; Reinhardt, 1983a; Kaifu, 1996).

However, opinions vary, and there is no generally accepted theory at present on the mechanisms of transformation of bite form with wear. It is self-evident that the *overbite* decreases with occlusal wear on the anterior teeth if the wear rate exceeds the rate of continuous tooth eruption. The question is why the *overjet* decreases with wear. If the above-mentioned incisor lingual tipping occurs to a greater degree in the maxillary anterior teeth than in the mandibular anterior teeth, without doubt this process plays a certain part in the decrease of *overjet*, as argued by Lysell and Fillipson (1958), Hasund (1965), Hylander (1977), Begg and Kesling (1977), and Varrela (1990).

The other views assume anterior shift of the whole mandibular dentition relative to the maxillary dentition with growth changes of the jaws (Begg, 1954; Begg and Kesling, 1977; Murphy, 1958; Selmer-Olsen, 1937; Reinhardt, 1983a). Murphy (1958) argued that edge-to-edge bite is achieved by forward shift of the mandibular dentition due to continuous condylar growth during adulthood. This view is supported in the study of Hylander (1977), but Lysell and Fillipson (1958) failed to detect supportive evidence. Another view is that the *overjet* is expected to decrease without changing mandibular shape if advanced occlusal wear results in an upward shift of the mandible relative to the maxilla with the condyles as a pivot (Selmer-Olsen, 1937; Reinhardt, 1983a; see Fig. 1 in Reinhardt, 1983a). This possibility has, however, not been demonstrated through examinations of actual data. In a sample of Australian Aboriginal skulls, Campbell (1925) observed no appreciable changes in the anteroposterior occlusal relation between the maxillary and mandibular first molars with advance of wear, and suggested that the mechanism of decrease of *overjet* lay in unknown local modification in the anterior dentition.

DESIGN OF THIS STUDY

The above review of the literature suggests the existence of the following dentoalveolar modification sequences with wear in populations with severe tooth wear. Both the maxillary and mandibular anterior teeth protrude forward to a certain extent and exhibit scissors bite during the formation period of the permanent dentition. With the advance of wear, the anterior teeth in both jaws gradually tip lingually to fill up interproximal spaces that would be generated by tooth wear, and to maintain contact relations between adjacent teeth in the anterior segment of the dentition, approaching to an orthognathous condition. The *overbite* decreases with occlusal wear and at the same time, the *overjet* decreases with wear to achieve edge-to-edge bite mainly because the amount of these inclination changes is larger in the maxillary than in the mandibular teeth.

In contrast, dentoalveolar morphology in populations with lighter tooth wear is interpreted, in the context of available information, as follows. Lingual tipping of the anterior teeth occur, if at all, only to a limited extent because a certain degree of loss of the mesiodistal crown diameter in the anterior teeth is a prerequisite of this change. Thus, scissors bite and a protrusive condition of the anterior teeth just after the accomplishment of dentition formation is maintained through adult life.

However, the model described above needs to be tested with respect to the following points. First, the wear parameters adopted in the previous demonstrations of incisor lingual tipping were not adequate. In the previous studies, the wear score on the molars or the average of wear scores on each tooth were used as the wear parameters, and incisor lingual tipping was demonstrated by examining interrelations be-

TABLE 1. Materials used in this study

Sample name	Period	Estimated age of the samples	Region	Sample size[1] M	F	Juv.	Total	Collection[2]
Jomon	Jomon (Prehistoric)	5000–300 BC	Hokkaido, Honshu, and Kyushu	48	25	5	78	TUM, NSM
Yayoi	Yayoi (Prehistoric)	300 BC–AD 300	Northern Kyushu and Yamaguchi	20	15	7	42	Kyushu Univ.
Kamakura	Kamakura (Medieval)	AD 1333	Kanto	55	35	8	98	TUM, NSM
Edo	Edo (Pre-modern)	1600 AD–1868 AD	Tokyo	46	29	6	81	NSM
Recent	Meiji-Taisho (Recent)	1868 AD–1926 AD	Unknown	36	12	2	50	TUM

M = males, F = females, juv. = juveniles.
[1] The number of sexed individuals (dental age ≥14 years) for the columns heading by M and F, and the number of individuals with unknown sex (dental age <14 years) for the column heading by juv.
[2] TUM = University Museum, Univ. of Tokyo; NSM = National Science Museum, Tokyo.

tween these wear parameters and incisor inclination angles. However, if incisor lingual tipping is supposed to be dependent on loss of mesiodistal diameters of the anterior teeth due to wear, wear on the anterior teeth should be used as the wear parameter. The balance of wear severity between the anterior and posterior teeth are not necessarily similar among various Holocene human populations, as indicated in a study of Japanese populations (Kaifu, 1999a).

Secondly, changes in adulthood have been the primary focus of most of the previous studies aimed at demonstrating dentofacial morphological changes with wear or age. Dentofacial morphological changes are, however, expected to occur with wear continuously from the growth period. Therefore, changes in the dentition formation period are also to be examined in a detailed investigation.

Third, changes in interproximal spaces with wear should be investigated quantitatively in order to confirm the hypothesis that lingual tipping of the anterior teeth plays a role in filling up interproximal spaces of the anterior arch.

Fourth, details of the transformation sequence in bite form with wear, and its covariation with changes in anterior tooth inclination have to be investigated. This is important in understanding actual mechanisms of attainment of edge-to-edge bite.

Finally, an important question remains as to whether incisor lingual tipping is a mechanism that is inherent in all living human populations, or is one that was possessed only by some ancient populations with severe tooth wear. The review of the previous studies indicated that incisor lingual tipping is not always detected in ancient populations exhibiting a certain degree of severe tooth wear (see above). Investigation of interpopulation variation is needed to confirm the universality of this mechanism. For this purpose, it is necessary to investigate the interrelation between interpopulation variation in the degree of lingual tipping of the anterior teeth and interpopulation variation in tooth wear severity. In other words, it is necessary to investigate whether the former is to be explained by the latter. Comparisons of the degree of lingual tipping of the anterior teeth among populations exhibiting various amount of tooth wear, which is assessed by the same method, is effective for this purpose. All the previous studies were reports on a single population, and this kind of interpopulation comparison has not been made to date.

Suitable samples in which these issues can be addressed are available in Japan. They consist of skeletal collections of populations from different periods, and exhibit various degrees of tooth wear severity from heavy (prehistoric hunter-gatherers) to light (premodern and recent periods). Interpopulation differences in severity and pattern of tooth wear for these samples have been investigated using the same scale by Kaifu (1999a).

MATERIALS AND METHODS

Materials

The materials used in this study and other relevant information are tabulated in Table 1. Hereafter, the terms Jomon, Yayoi, Ka-

makura, Edo, and Recent are used in this paper to refer to samples from the Jomon to Recent periods.

The Jomon people were prehistoric hunter-gatherer-fishers of Japan during the period between ca. 10,000–300 BC. The major portion of the current collection is from shell-mounds of the Middle to Final Jomon periods (ca 3,500–300 BC) along the coast of the Kanto district. The Yayoi sample is composed of populations from northern Kyushu and neighboring Yamaguchi Prefecture (western Japan). These prehistoric rice agriculturists and metal-working people are considered to be immigrants from the Asian continent or their offspring (Nakahashi, 1993, and others). Recent studies have shown that the later Mainland Japanese evolved through the mixture of this population and native Jomon people, possibly with greater influence from the former (see Hudson, 1999 for details). The entire Kamakura sample of this study is derived from the Zaimokuza site in the southern Kanto region, which is considered to have been a temporary mass burial for war dead from a battle in 1333 (Mikami, 1956). The Edo sample consists of remains from ordinary burials excavated in the city of Edo (present day Tokyo). The Recent sample is comprised of specimens derived from dissecting rooms. More detailed information of these chronological populations are available in Kaifu (1999a).

Antemortem tooth loss, significant loss of the crown by caries, and tooth dislocation due to periodontitis may affect the original dentoalveolar morphology. Among dentally adult specimens with not more than three such abnormal teeth in both maxillary and mandibular dentitions anterior to the third molars, those judged as preserving unaffected dentoalveolar morphology at least on one side were selected. In addition, among specimens whose mandible is missing, those with an intact maxillary dentition anterior to the third molars were added to the sample if there was no sign of the existence of abnormal teeth in the missing mandible. This judgement was done on the basis of continuity and symmetry of occlusal wear and presence or absence of extraerupted teeth in the maxillary dentition. Extraeruption of a tooth occurs when it loses its antagonist(s) (Anneroth and Ericson, 1967; Compagnon and Wada, 1991) and hence is a useful indicator of antemortem tooth loss in the opposing dentition. Among the entire materials selected, about 60% were almost complete specimens with no abnormal teeth in the dentition anterior to the third molars.

Sexes were determined by the author mainly based on the pelvis and cranial morphology for every individual with dental age of 14 or more. Dental age was judged for subadult specimens with reference to Ubelaker (1989, Fig. 71), from 7 to 20.5 years with an interval of 0.5 years. The dental development sequence for Japanese populations has not been sufficiently investigated so far, and Ubelaker's chart, which was compiled from the data of Native Americans and other "non-American White" populations for the purpose of studies of Native Americans, is considered to be the best substitute.

Methods

All the measurements were taken from lateral photographs magnified 1.5 times real size. Photography was conducted using a Nikkor telephoto lens system keeping the distance between the subject and camera at 3 m to minimize the parallax effect. The reference lines were defined on the photographs as in Figure 1, and the angular measurements were defined as in Table 2. Details of the definitions of the reference lines, landmarks, and measurements along with their rationale are available in Kaifu (1999b).

Changes of the tooth inclination angles, *overbite*, and *overjet* accompanied with the advance of wear on the central incisors were examined by bivariate analyses. Changes in the observed frequency of interproximal spacing accompanied with wear were also investigated. All the statistical procedures were conducted using SYSTAT 5.2.1 for Macintosh (SYSTAT, Inc., 1992).

Variation in anteroposterior occlusal relations between the maxillary and mandibular molars obviously affects the value of *overjet*. Because this factor may also affect other variables used in this study, such as incisor inclination angles, variation of this trait is taken into consideration in the present analyses. In this study, anteroposterior

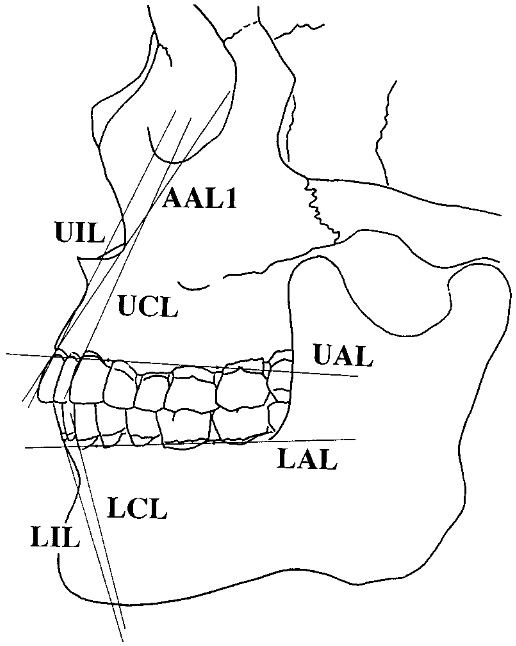

Fig. 1. Reference lines used in this study. Following are brief definitions for these lines: UAL (LAL) is the straight line passing through the point situated on the border between the lateral and inferior (superior) surfaces of the alveolar process at C/P1, and the similar point at M1/M2; AAL1 is the straight line passing through the most anterior point on the border between the maxillary alveolar bone and I^1, tangent to the infero-posterior margin of the nasal orifice; UIL (LIL, UCL, or LCL) is the straight line representing the inclination of the contour of the cervical portion of the anterior surface of I^1 (I_1, C^1, or C_1) root that exposes from the alveolar bone. See Kaifu (1999b) for details.

TABLE 2. List of angle measurements

Measurements	Definitions[1]
Alveolar inclination angle 1	Angle formed by AAL1 and UAL
I^1 inclination angle	Angle formed by UIL and UAL
C^1 inclination angle	Angle formed by UCL and UAL
I_1 inclination angle	Angle formed by LIL and LAL
C_1 inclination angle	Angle formed by LCL and LAL

[1]See Figure 1 for definitions.

molar relation is judged by visual inspection of the original skulls on the basis of position of the mesiolingual cusp of the maxillary first molar when both dentitions are positioned in centric occlusion (maximum intercuspation). This method is essentially the same as the common method proposed by

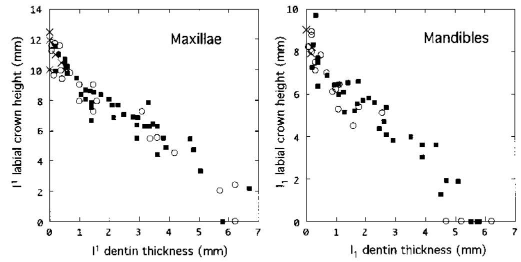

Fig. 2. Scatterplots and linear regression lines of *I1 dentin thickness* and *I1 labial crown height* for the Jomon. Solid squares = males. Open circles = females. x = specimens with unknown sex (dental age < 14).

Baume et al. (1970) in which the molar relation is judged in lateral aspect of the buccal segments. Taking existence of side differences into consideration, in this study, Class I was defined as a condition where the mesiolingual cusps of the maxillary first molars occlude to the central fovea on the mandibular first molars in both sides; Class II was a condition where, on the average of both sides, the maxillary first molars occlude more anteriorly than the Class I condition, while Class III indicated the opposite condition to Class II. Rare cases where each side shows a similar degree of Class II and Class III molar relations were also discriminated.

RESULTS

Figure 2 shows the interrelation between labiolingual thickness of the exposed dentin and buccal crown height of the central incisors for the Jomon sample. The degree of actual occlusal wear for a certain value of the *I1 dentin thickness* can be determined from this figure. For example, the crown height of the maxillary central incisor reduced to 50% of its initial condition when the *I^1 dentin thickness* reaches about 3 mm on average. The relation between the *I1 dentin thickness* and crown height for the other samples was approximately the same with that observed in the Jomon, though the range of *I1 dentin thickness* is less in the other samples than in the Jomon.

Scatterplots between angle variables and *I^1 dentin thickness* for the Jomon (dental age ≥ 14) are shown in Figure 3. Figure 4 includes scatterplots between *I^1 inclination angle* or *C^1 inclination angle* and *I1 dentin thickness* for selected samples other than

the Jomon. Each sample was divided into light- and heavy-wear groups with the median of *I1 dentin thickness* as the boundary. Table 3 shows the results of a Mann-Whitney *U* test for each angle variable between the two groups, as well as ranges of *I1 dentin thickness* and coefficients of determination. Regression analyses were not performed because the changes in the Jomon were not linear (see below), and the coefficients of determination are generally low (Table 3). Also, this method tends to be best-fitted to the last observation in this series and is heavily influenced by outliers. As far as Figure 3 and 4 indicate, in most cases, variation in anteroposterior molar relation do not affect the angle variables in a consistent manner. It is possible, however, that the molar relation has a significant influence on the angle variables at the individual level.

Figure 5 shows variations of selected angle variables for two age groups of subadult subsamples (7–14 and 14–20.5 years). These data can be regarded approximately as values of the angle variables just after the eruption of the permanent anterior teeth, or “initial values” for the permanent anterior teeth. Descriptive statistics and results of statistical tests for these subsamples are tabulated in Table 4. As for the Jomon and Yayoi samples in which tooth wear is comparatively severe, a group of points at the left end of Figure 3 and 4 can be regarded as “adolescent values.” Assessment of sex differences is impossible for “initial values,” while it is possible for “adolescent values.”

Figure 6 is scatterplots between *overbite*, *overjet*, and *I^1 dentin thickness* within each sample (dental age ≥ 14). As expected, individuals with Class II molar relations generally show larger *overjet* values than the other individuals.

The number of interproximal spaces observed in the anterior segment of the maxillary and mandibular dentitions anterior to the canines were counted for each individual, and the results were tabulated in Table 5–9. In Table 5–9, each sample was subdivided into subadult (dental age between 14 and 20.5) and adult subsamples, the latter of which was further divided according to the value of *I1 dentin thickness*. The materials included here were those

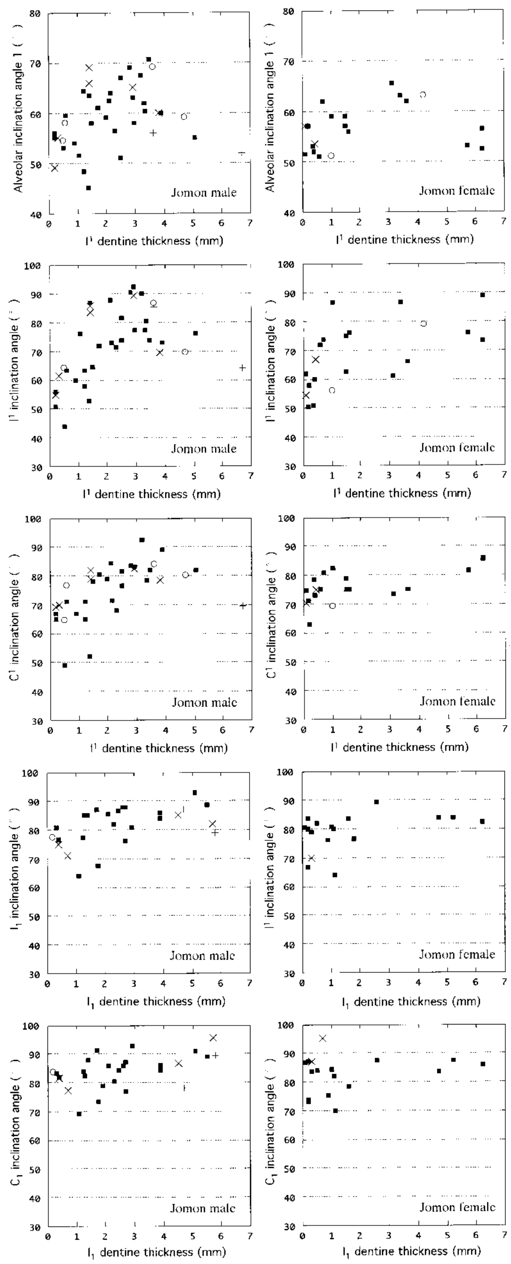

Fig. 3. Scatterplots of the dentoalveolar lateral inclination angles and *I1 dentin thickness* for the Jomon (dental age ≥ 14). Solid squares = Class I. × = Class II. + = Class III. Open circles = AP molar relation unknown. Stars = specimens showing a similar degree of Class II and Class III molar relations in each side.

specimens with no antemortem tooth loss or marked dental diseases (N = 194). In addition to these, among those specimens whose mandible is missing, those with an intact

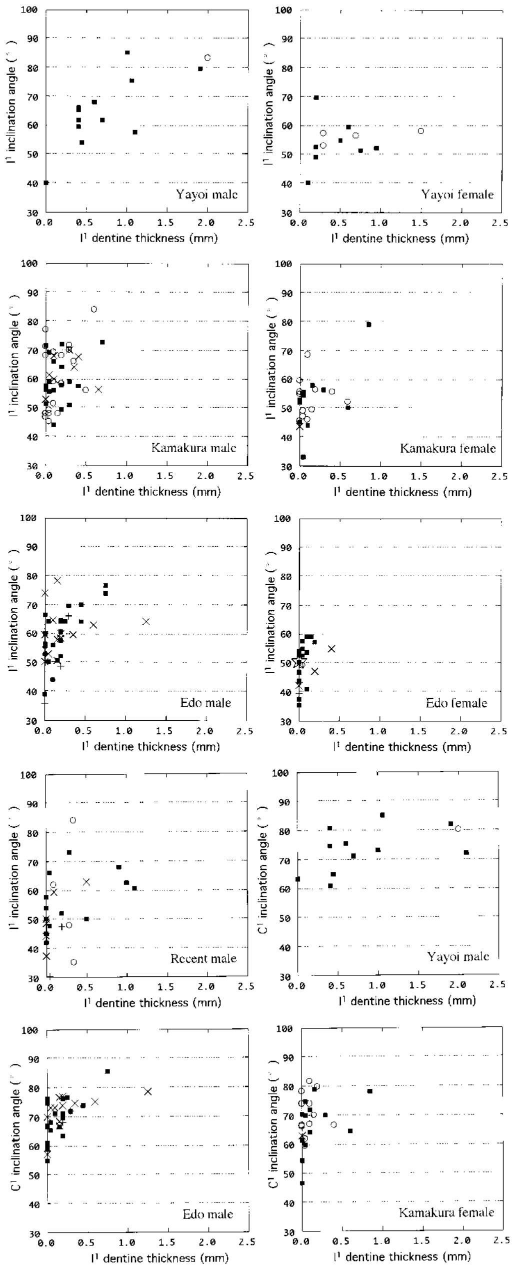

Fig. 4. Scatterplots of the *I^1* or *C^1 inclination angles* and *I1 dentin thickness* for the selected samples from the Yayoi, Kamakura, Edo, and Recent (dental age ≥ 14). Symbols as in Fig. 3.

maxillary dentition anterior to the third molar were added to the sample if there was no sign of the existence of abnormal teeth in the missing mandible judged by the method described in the section of "Materials" (N = 37). Although all the teeth need to be preserved in counting spaces, they were counted where possible referring to other circumstances such as the condition of interproximal contact facets. The spacing due to crowding or abnormal position of the teeth, which were sporadically observed in the Edo and Recent samples, was not counted.

Jomon

Figure 3 and Table 3 indicate that both the maxillary and mandibular anterior teeth of the Jomon males tip lingually with the advance of wear, eventually reaching a nearly upright condition. Likewise, the anterior surface of the maxillary alveolar bone retroclines with wear. However, these inclination angles seem to reach the maxima, as for the maxillary central incisors, when the teeth are worn to the stage where *I^1 dentin thickness* becomes about 2 mm (a stage where the crown height reduces to about 70% of its initial condition; Fig. 2), and as for the mandibular central incisors, when they are worn to the stage where *I_1 dentin thickness* becomes about 3 mm (a stage where the crown height reduces to about 50% of its initial condition; Fig. 2). The lingual tipping of the maxillary canines occurs more slowly compared with the maxillary central incisors and it continues to the time when the initial crown height of the maxillary canines reduces to about 50%. In cases where the wear advances further, the inclination angles of the anterior teeth and anterior surface of the maxillary alveolar bone tend to remain unchanged or, in some cases, more or less procline, though the sample size is too small to confirm these tendencies. Although the degree of change is somewhat less, similar tendencies are observed in the Jomon females except for the mandibular canines. Reduction of the *alveolar inclination angle 1* with wear in the Jomon females becomes significant if the three individuals with extremely advanced wear are excluded from the sample ($p = 0.04$).

With regard to differences between the jaws in the Jomon sample, the initial values of *I1 inclination angles* are smaller in the maxilla than in the mandible by about 20° in both sexes. Both maxillary and mandibular central incisors become nearly upright with the advance of wear, so that the amount of

TABLE 3. Results of the two-tailed Mann-Whitney U test, ranges of I1 dentine thickness (I1DT), and coefficients of determination (r^2) for the angular measurements

	Males					Females				
	AIA1	I^1IA	C^1IA	I_1IA	C_1IA	AIA1	I^1IA	C^1IA	I_1IA	C_1IA
Jomon										
N	39	37	34	26	27	21	21	19	17	17
P of M-W *U* test	0.04	0.00	0.00	0.01	0.02	0.13	0.01	0.07	0.12	0.96[1]
Range of I1DT	0.2–6.7	0.2–6.7	0.2–6.7	0.2–5.8	0.2–5.8	0.1–6.2	0.1–6.2	0.1–6.2	0.1–6.2	0.1–6.2
r^2	0.06	0.20	0.26	0.25	0.24	0.04	0.35	0.41	0.16	0.05
Yayoi										
N	14	13	12	10	10	14	12	11	6	6
P of M-W *U* test	0.95[1]	0.04	0.12	0.91	0.34[1]	0.70	0.52	0.58[1]	0.81[1]	0.06[1]
Range of I1DT	0.0–2.1	0.0–2.0	0.0–2.1	0.2–5.5	0.2–5.5	0.1–1.5	0.1–1.5	0.1–1.0	0.3–0.8	0.3–0.8
r^2	0.05	0.57	0.25	0.04	0.44	0.01	0.04	0.05	0.00	0.21
Kamakura										
N	45	45	44	20	23	27	25	26	11	13
P of M-W *U* test	0.09	0.18	0.31	0.49[1]	0.39[1]	0.05	0.14	0.02	0.70	0.24
Range of I1DT	0.0–0.7	0.0–0.7	0.0–0.7	0.0–1.1	0.0–1.1	0.0–0.9	0.0–0.9	0.0–0.9	0.0–0.6	0.0–0.8
r^2	0.17	0.10	0.02	0.07	0.01	0.25	0.23	0.07	0.01	0.19
Edo										
N	40	40	37	28	34	22	22	20	20	19
P of M-W *U* test	0.07	0.02	0.00	0.61	0.33	0.97	0.01	0.91[1]	0.54[1]	0.93
Range of I1DT	0.0–1.3	0.0–1.3	0.0–1.3	0.0–2.2	0.0–2.2	0.0–0.4	0.0–0.4	0.0–0.4	0.0–1.2	0.0–1.2
r^2	0.06	0.20	0.36	0.01	0.03	0.00	0.16	0.00	0.01	0.02
Recent										
N	26	26	23	22	21	9	9	6	8	8
P of M-W *U* test	0.20	0.02	0.81	0.60*	0.03[1]	0.62	0.54*	0.05*	0.77[1]	0.88
Range of I1DT	0.0–1.1	0.0–1.1	0.0–1.1	0.0–1.8	0.0–1.8	0.0–0.5	0.0–0.5	0.1–0.5	0.1–0.9	0.1–0.9
r^2	0.05	0.17	0.00	0.02	0.08	0.08	0.00	0.09	0.08	0.03

[1] Measurement increases with wear as a whole. A probability without an asterisk indicates the opposite.

change of the inclination angles is far greater in the maxillae (about 30°) than in the mandibles (about 10°). A similar trend is seen in the male canines though the degree of change is smaller than that of the central incisors. (The amounts of change are about 15° for the maxillary canines and a few degrees for the mandibular antagonists.) The amounts of change are not clearly different between the maxillary and mandibular canines of the Jomon females.

While there are no clear sex differences in the dental inclination angles in adolescence, the amounts of lingual tipping during adulthood tend to be somewhat smaller in the females than in the males, except for the mandibular canines. Consequently, the anterior teeth become nearly upright with the advance of occlusal wear in the males, while they reach not more than about 80° in the females. The same observation applies to the anterior surface of the maxillary alveolar process; while adolescent values are nearly equal, the amount of change is larger in the males than in females.

With regard to the transition of bite form (Fig. 6), the Jomon show scissors bite (*overbite* > 0, *overjet* > 0) in the earlier stage of formation of the permanent dentition. While the *overbite* and *overjet* decrease with the advance of wear subsequently, the former reaches zero earlier than the latter and thus the Jomon individuals pass through the condition of *overbite* $= 0$ and *overjet* > 0 before reaching the edge-to-edge bite condition (*overbite* $= 0$, *overjet* $= 0$). The *overbite* reaches zero when the *I^1 dentin thickness* becomes about 1 mm, and this is the stage when the crown height reduces to about 80% of its initial condition (Fig. 2). The *overjet* does so when the *I^1 dentin thickness* becomes about 2 mm, and this coincides with the time when the maxillary central incisors become nearly upright (Fig. 3). Either or both *overbite* and *overjet* show negative value(s) in some specimens with further advanced wear. If the anterior growth of the mandible contributes significantly to decrease of the *overjet*, the anteroposterior molar relations are expected to shift toward the Class III condition. Such a tendency is, however, not observed in the results of this study (Fig. 3).

As for interproximal spacing (Table 5), while observation frequencies of individuals with spaces are moderate in subadult subsamples as far as the females whose sample

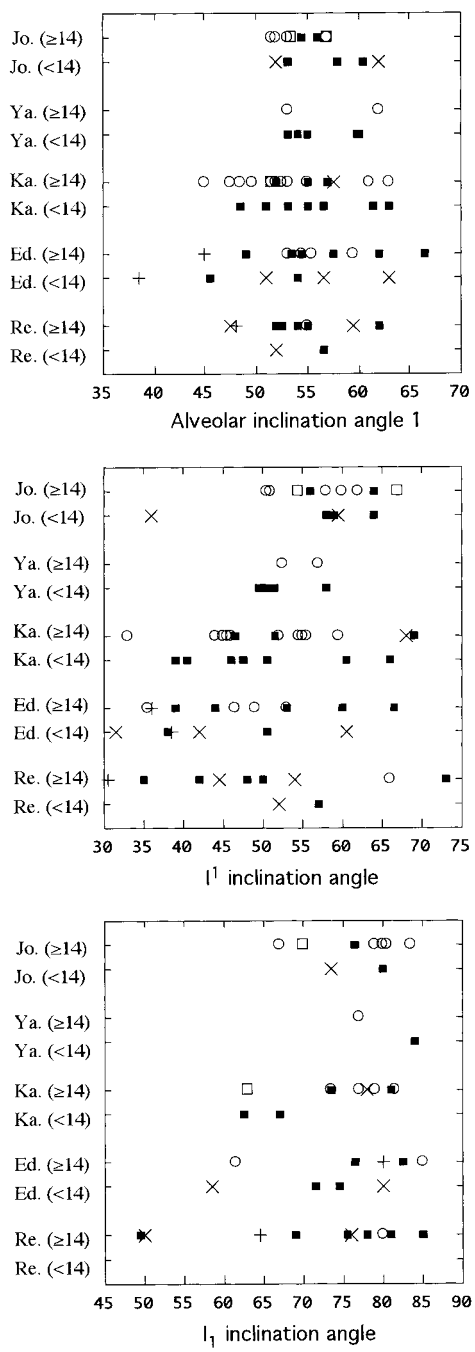

Fig. 5. Dentoalveolar inclination angles for the subadult subsamples (grouped by dental age). Symbols for the specimens with dental age of 14 or more are as follows: Solid squares = males with Class I. × = males with Class II. + = males with Class III. Open circles = females with Class I. Open squares = females with Class II. Symbols for the specimens with dental age less than 14 are as follows: Solid squares = Class I. × = Class II. + = Class III.

size is relatively large is concerned, the spaces are rare in adults with light or moderate occlusal wear in both jaws and sexes. On the other hand, in the adult male mandibles whose sample size is relatively large, the observation frequency of spaces apparently increases with the advance of wear. The same observations seem to apply to the smaller samples of the male maxillae and the females. This increase of the frequencies of spaces in the anterior segment of the dentition becomes apparent after the stage when the lingual tipping of the central incisors reached the maximum conditions (see above).

Figure 7 is a series of Jomon specimens showing modification of the anterior dentoalveolar complex with wear described above. Figure 8 shows two representative Jomon specimens exhibiting above-described relation between tooth wear and interproximal spaces.

The Yayoi and later populations

Inclination of anterior teeth. A slight degree of lingual inclination of the anterior surface of the maxillary alveolar process with wear is observed in both sexes of the Kamakura and the Edo males (Fig. 4 and Table 2).

As for the maxillary anterior teeth, the Yayoi males show lingual tipping of the maxillary central incisors to an extent which approaches the Jomon condition, accompanied with occlusal wear that reaches about 2 mm in *I^1 dentin thickness*. The maxillary canines of the Yayoi males also seem to show a slight lingual tipping. In the Yayoi females and the samples after the Yayoi periods, the *I^1 dentin thickness* reaches only up to about 1 mm. Nevertheless, at least very small amounts of lingual tipping with wear are generally recognized in the maxillary anterior teeth of every sample, except the Yayoi and Recent female samples whose sample sizes are small. This tendency is particularly clear, among these samples, in the Edo males in that lingual tipping is seen in both the maxillary central incisors and canines and the coefficients of determination are generally larger than for the others.

The mandibular anterior teeth do not show lingual tipping in a statistically significant manner in all the samples in and after the Yayoi period. In contrast, the Recent males show a statistically significant tendency of labial tipping in the mandibular canines.

TABLE 4. Descriptive statistics of the angular measurements for subadult subsamples

Variables	Jomon N	Jomon M (s.d.)	Yayoi N	Yayoi M (s.d.)	Kamakura N	Kamakura M (s.d.)	Edo N	Edo M (s.d.)	Recent N	Recent M (s.d.)
Alv. inc. angle	14	55.5 (3.3)	7	56.7 (3.8)	26	54.2 (5.0)	19	54.5 (6.7)	13	53.9 (4.0)
I^1 inc. angle	14	57.1 (7.7)	7	52.9[1] (3.3)	21	51.2[1] (9.6)	16	46.5[1] (10.2)	12	50.2[1] (11.9)
C^1 inc. angle	13	70.7 (5.2)	3	71.7 (5.4)	20	66.8 (7.4)	12	62.2[3] (6.9)	10	62.4[1] (8.3)
I_1 inc. angle	9	76.7 (5.4)	2	80.5 (5.0)	11	74.1 (7.0)	9	74.4 (9.2)	10	70.9 (12.6)
C_1 inc. angle	10	82.1 (9.8)	1	80.0 (—)	9	82.4 (4.6)	12	80.7 (5.7)	7	77.6[2] (4.5)

[1] Significantly smaller than the Jomon ($P < 0.05$) in Mann-Whitney U tests.
[2] Significantly smaller than the Kamakura ($P < 0.05$) in Mann-Whitney U test.
[3] Significantly smaller than the Jomon, Yayoi, and Kamakura ($P < 0.05$) in Mann-Whitney U test.

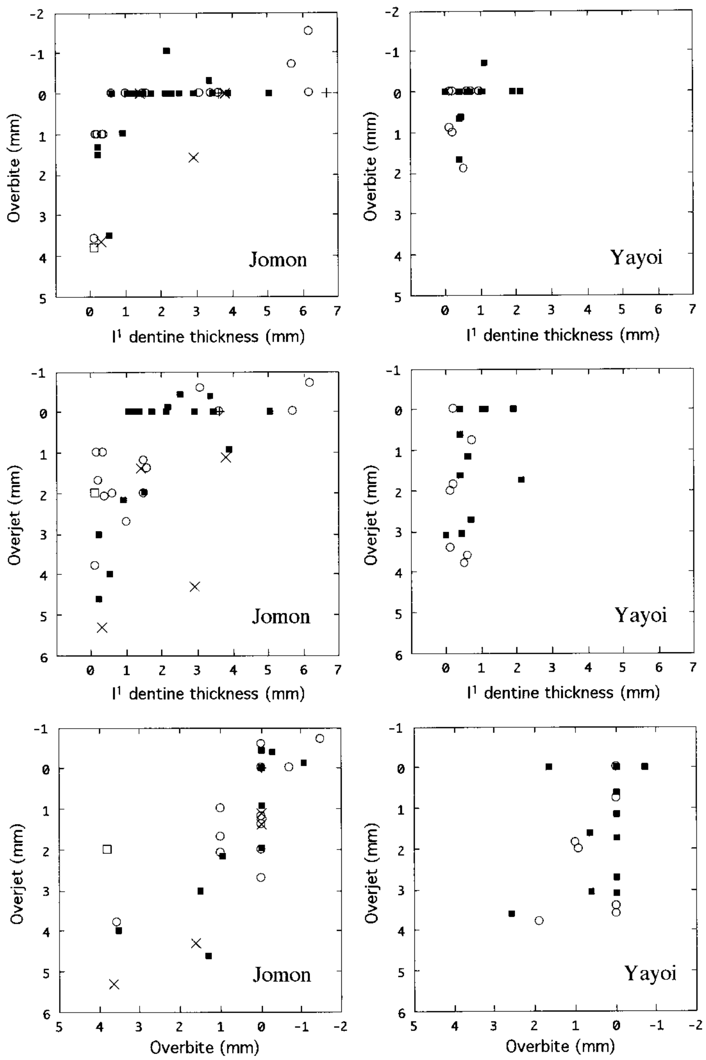

Fig. 6. Scatterplots of the *I^1 dentin thickness*, *overbite*, and *overjet* (dental age ≥ 14). The number of individuals with edge-to-edge bite (*overbite* = 0 and *overjet* = 0) is ten for the Jomon and four for the Yayoi. Solid squares = males with Class I. × = males with Class II. + = males with Class III. Open circles = females with Class I. Open squares = females with Class II. Open triangles = females with Class III.

Initial values of anterior tooth inclination angles. The five chronological samples from the Jomon to Recent are similar in the means of the initial values of *alveolar inclination angle 1* (about 55°), though these values are somewhat more variable in the Kamakura, Edo, and Recent than in the Jomon and Yayoi samples (Fig. 5 and Table 4). With regard to the initial values for the *I^1 inclination angle*, the Ka-

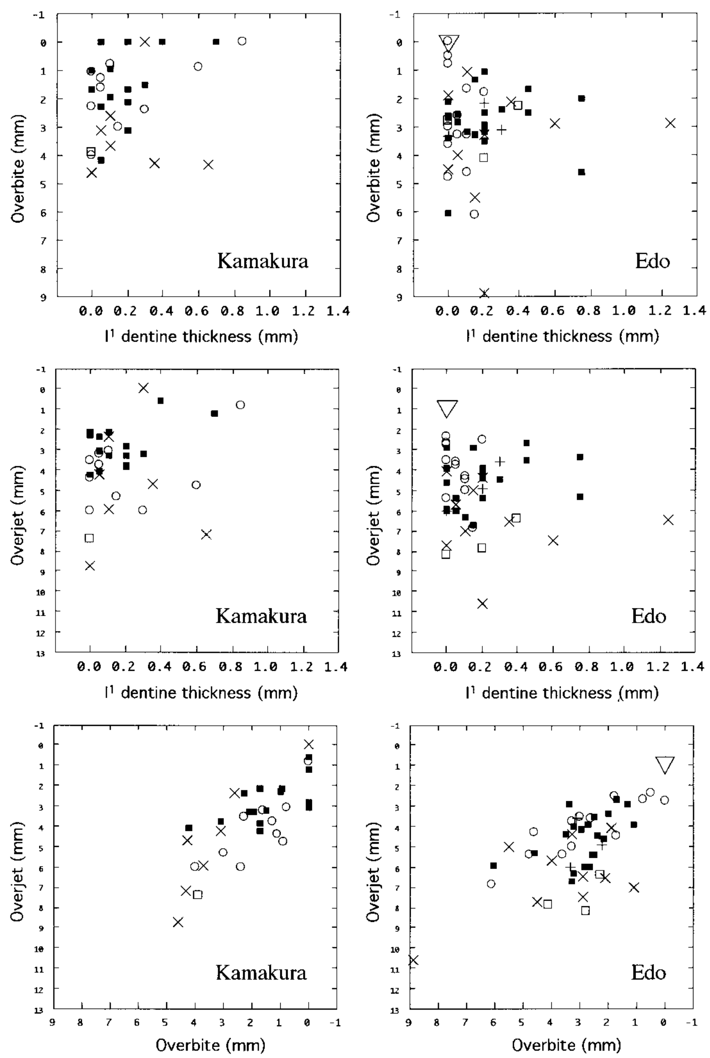

Fig. 6

makura, Edo, and Recent specimens are more variable than the Jomon and Yayoi, and include individuals with more protrusive tendencies. The same observation applies to the Edo and Recent for the canines. While the Yayoi maxillary central incisors are somewhat smaller in the initial values of the inclination angle than the Jomon, the Yayoi does not includes individuals with further smaller values as are observed in the Kamakura, Edo, and Recent groups. Although a similar tendency toward a more protrusive condition through time is observed in the initial values of the mandibular anterior teeth, most of the differences between the chronological samples are not statistically significant.

Bite form. In the Yayoi sample, the *overbite* decreases with wear and becomes zero when the *I^1 dentin thickness* reaches about 1 mm as in the case of the Jomon, but *I^1 dentin thickness* rarely exceeds 2 mm and the *overjet* remains positive in most of the specimens (Fig. 6). In the three chronological samples after the Yayoi period, occlusal wear on the central incisors is very slight and the initial condition of scissors bite is

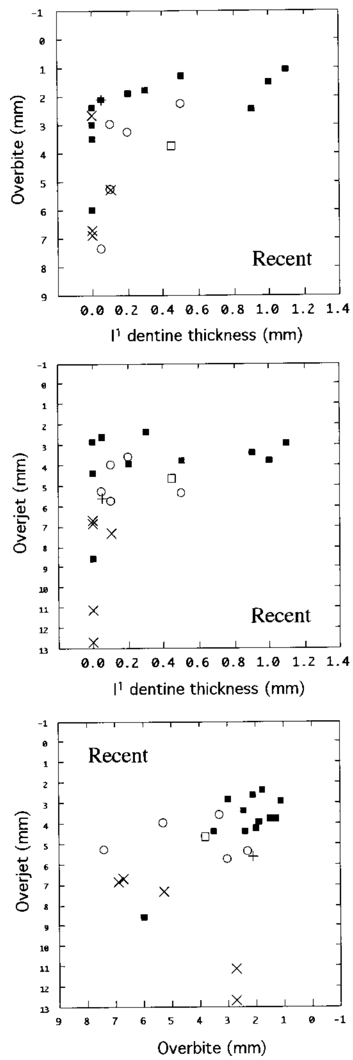

Fig. 6

maintained in most individuals. The *overbite* slightly decreases with wear in the Kamakura and Recent, while this tendency is not clear in the Edo sample. There are no appreciable changes in the *overjet* with wear in these three samples. Although severity of wear on the maxillary central incisors is similar among these three samples (Kaifu, 1999a), the *overbite* and *overjet* of the Edo and Recent are generally greater than those of the Jomon, Yayoi, and Kamakura specimens.

Interproximal spacing. Although the sample sizes are not enough to point out intergroup differences clearly, the following tendencies are generally recognized from the results tabulated in Tables 5–9. The spaces are rare in both jaws and sexes in the Yayoi adults. The frequency of spaces in the Kamakura is high, in both sexes and both subadults and adults, compared to the conditions seen in the Jomon, Yayoi, and Edo samples (see Fig. 8). This is especially true in the maxillary dental arch. The spaces are rare in the Edo compared to the Kamakura groups in both subadults and adults. While spaces are occasionally observed in the Recent maxillae, those in the mandibles are rare.

DISCUSSION

Lingual tipping in populations with severe wear

The Jomon are a population that shows severe wear across the entire dentition (Kaifu, 1999a). This study revealed that the anterior teeth of both jaws tip lingually with wear so far as to become nearly upright. At the same time, the anterior surface of the maxillary alveolar process also inclines lingually to a certain extent. In this population, a great degree of loss of mesiodistal tooth crown dimensions occurs accompanied with occlusal wear in both the anterior and posterior segments of the dentition. The sum of loss from I1–M1 on one side in the Jomon during the period in which most of the teeth are retained amounts to about 10 mm (Kaifu, 1999a). Nevertheless, interproximal spaces rarely occur in the adult dentition while the anterior teeth tip lingually. These observations indicate that, as argued by Selmer-Olsen (1937), Lysel (1958), Hasund (1965), and Hylander (1977), the lingual tipping of the anterior teeth plays a role in filling up interproximal spaces that would be generated by wear and in maintaining contact relations between adjacent teeth in the anterior segment of the dentition. However, the amount of lingual tipping of the anterior teeth was somewhat less in the females than in the males in the Jomon sample. While degree of anterior tooth protrusion is similar between both sexes during the developmental period, this difference in the amount of

TABLE 5. Observed frequency of individuals for the number of interproximal spaces in the dentition anterior to the canine (Jomon)[1]

	Males							Females						
N of spaces	0	1	2	3	4	5	Total	0	1	2	3	4	5	Total
Maxillae														
Subadults	1					1	2	2	1	1	1	1		6
$0 \leq I^1$ dent. t.[2] < 0.2							0							0
$0.2 \leq I^1$ dent. t. < 0.5	1						1							0
$0.5 \leq I^1$ dent. t. < 1.0	3	1					4	2						2
$1.0 \leq I^1$ dent. t. < 2.0	3		1				4	2						2
$2.0 \leq I^1$ dent. t. < 3.0	5						5							0
$3.0 \leq I^1$ dent. t. < 4.0	3	1		1			5	1						1
$4.0 \leq I^1$ dent. t.						1	1				1			1
Mandibles														
Subadults	1						1	1	1		2	1		5
$0 \leq I_1$ dent. t. < 0.2							0							0
$0.2 \leq I_1$ dent. t. < 0.5	3						3							0
$0.5 \leq I_1$ dent. t. < 1.0							0	1		1				2
$1.0 \leq I_1$ dent. t. < 2.0	6						6	2						2
$2.0 \leq I_1$ dent. t. < 3.0	3						3	1						1
$3.0 \leq I_1$ dent. t. < 4.0							0							0
$4.0 \leq I_1$ dent. t.				2		3	5						1	1

[1] See text for detailed explanation.
[2] dent. t. = dentin thickness.

TABLE 6. Observed frequency of individuals for the number of interproximal spaces in the dentition anterior to the canine (Yayoi)[1]

	Males							Females						
N of spaces	0	1	2	3	4	5	Total	0	1	2	3	4	5	Total
Maxillae														
Subadults							0	1					1	2
$0 \leqq I^1$ dent. t. < 0.2	1						1	1						1
$0.2 \leqq I^1$ dent. t. < 0.5	4						4	3						3
$0.5 \leqq I^1$ dent. t. < 1.0	2						2	3						3
$1.0 \leqq I^1$ dent. t. < 2.0	3						3	1						1
$2.0 \leqq I^1$ dent. t. < 3.0	1		1				2							0
Mandibles														
Subadults							0				1			1
$0 \leqq I_1$ dent. t. < 0.2							0							0
$0.2 \leqq I_1$ dent. t. < 0.5	5						5	2						2
$0.5 \leqq I_1$ dent. t. < 1.0	2						2	2						2
$1.0 \leqq I_1$ dent. t. < 2.0	2			1			3	1						1
$2.0 \leqq I_1$ dent. t. < 3.0	1						1							0
$3.0 \leqq I_1$ dent. t. < 4.0							0							0
$4.0 \leqq I_1$ dent. t.				1			1							0

[1] See text for detailed explanation.
[2] dent. t. = dentin thickness.

change leads to the sexual dimorphism in anterior tooth protrusion in adulthood in this population (Kaifu, 1999a).

The results of this study suggest that interproximal spaces occur in the anterior segment of the Jomon dentition after the stage when the anterior teeth attained a nearly upright condition with the advance of wear. Begg (1954) made a similar observation in Australian Aboriginal skulls and concluded that "mesial tooth migration is greatly retarded or seems almost to have ceased" in senile individuals, because he thought at that time that mesial tooth migration is the primary compensatory mechanism for interproximal spaces produced by wear. These observations, however, seem to indicate that, in the anterior segment of the dentition, lingual tipping of the anterior teeth contribute in large part to maintaining contact relations between adjacent teeth, and mesial tooth migration does this far less. This view is supported by the results of the following examination on the changes in

TABLE 7. Observed frequency of individuals for the number of interproximal spaces in the dentition anterior to the canine (Kamakura)[1]

	Males							Females						
N of spaces	0	1	2	3	4	5	Total	0	1	2	3	4	5	Total
Maxillae														
Subadults	2		2			1	5	6				1	2	9
$0 \leqq I^1$ dent. t.[2] < 0.2	11	1	3	1	1	3	20	5	1	1	1	1	1	10
$0.2 \leqq I^1$ dent. t. < 0.5	12			2			14				1		2	3
$0.5 \leqq I^1$ dent. t. < 1.0	3						3	2						2
Mandibles														
Subadults	1					1	2	5					1	6
$0 \leqq I_1$ dent. t. < 0.2	2						2	1	1				1	3
$0.2 \leqq I_1$ dent. t. < 0.5	6			1	1		8	2			1	1		4
$0.5 \leqq I_1$ dent. t. < 1.0	4					1	5	2						2
$1.0 \leqq I_1$ dent. t. < 2.0	2						2							0

[1] See text for detailed explanation.
[2] dent. t. = dentin thickness.

TABLE 8. Observed frequency of individuals for the number of interproximal spaces in the dentition anterior to the canine (Edo)[1]

	Males							Females						
N of spaces	0	1	2	3	4	5	Total	0	1	2	3	4	5	Total
Maxillae														
Subadults	4				1		5	3						3
$0 \leqq I^1$ dent. t.[2] < 0.2	10	1	2		1		14	9	2	1			1	13
$0.2 \leqq I^1$ dent. t. < 0.5	12						12	2					1	3
$0.5 \leqq I^1$ dent. t. < 1.0	1						1							0
Mandibles														
Subadults	3						3	5						5
$0 \leqq I_1$ dent. t. < 0.2	3						3	5		2		1		8
$0.2 \leqq I_1$ dent. t. < 0.5	13	1		1			15	7						7
$0.5 \leqq I_1$ dent. t. < 1.0	5			1			6	1						1
$1.0 \leqq I_1$ dent. t. < 2.0	1		1				2	1						1

[1] See text for detailed explanation.
[2] dent. t. = dentin thickness.

dental arch breadths between the right and left second incisors and canines (external breadths measured at the cementoenamel junction). The Jomon male specimens were divided into light- and heavy-wear groups on the basis of the values of *I^1 dentin thickness*. The boundary was set at 2 mm because the sample was divided into approximate halves by this value. Results of the Mann-Whitney *U* test between the two groups indicated that the differences in dental arch breadths were not significant (probabilities were 0.27, 0.64, 0.64, and 0.78 for the four arch breadths in both jaws; sample sizes were 18–23). The Jomon female sample was excluded from this analysis because of small size. Hylander (1977) also obtained nonsignificant results in his analysis of a sample of Native Americans.

My findings suggest that the inclination of anterior teeth of the Jomon do not change in a consistent manner after the attainment of a nearly upright state, but maintain an upright state or even tip labially in some individuals. This phenomenon is probably explained as follows. The long axis of an anterior tooth with severe occlusal wear is easily changed by occlusal forces because of enlargement of the occlusal surfaces and reduction of length of the root supported by the alveolar bone due to continuous eruption (cf. Reinhardt, 1983b; Clarke and Hirch, 1991b).

Edge-to-edge bite

Several mechanisms to decrease the *overjet* and attain edge-to-edge bite have been proposed and discussed by previous workers, as mentioned above. This study revealed that while the anterior teeth of the Jomon tip noticeably lingually with wear, the amount of change is greater in the

TABLE 9. Observed frequency of individuals for the number of interproximal spaces in the dentition anterior to the canine (Recent)[1]

	Males							Females						
N of spaces	0	1	2	3	4	5	Total	0	1	2	3	4	5	Total
Maxillae														
Subadults	4			1		1	6	1						1
$0 \leqq I^1$ dent. t.[2] < 0.2	6	1	1			1	9			1	1			2
$0.2 \leqq I^1$ dent. t. < 0.5	1			1			2	2				1		3
$0.5 \leqq I^1$ dent. t. < 1.0	2						2	1						1
$1.0 \leqq I^1$ dent. t. < 2.0		1					1							0
Mandibles														
Subadults	6						6							0
$0 \leqq I_1$ dent. t. < 0.2	4	1					5	2						2
$0.2 \leqq I_1$ dent. t. < 0.5	3	1					4	4						4
$0.5 \leqq I_1$ dent. t. < 1.0	1						1	1						1
$1.0 \leqq I_1$ dent. t. < 2.0	2						2							0

[1] See text for detailed explanation.
[2] dent. t. = dentin thickness.

maxillary central incisors by about 20° than in their mandibular antagonists. This observation is consistent with the results obtained in a study of Native American skulls by Hylander (1977). In addition, the results of the present study indicated that the time of attainment of zero *overjet* in the Jomon sample approximately coincides with the time when their maxillary central incisors reached a nearly upright state. These observations indicate that the decrease and disappearance of *overbite* and *overjet* is caused fundamentally by tooth wear and accompanied lingual tipping of the anterior teeth. Because the effect of this process is apparently great, the probable contribution of the other factors to the decrease of *overjet* is limited, if at all.

Among the other possible contributing factors in decrease of the *overjet*, a slight degree (about 5°) of anterior rotation of the mandible with wear was suggested to have occurred in the Jomon sample of this study (Y. Kaifu, unpublished data). Therefore, this factor may contribute in some way to the decrease of *overjet*. On the other hand, the anterior movement of the mandibular dental arch relative to the maxillary dental arch was not detected in the present analyses of the Jomon sample.

Universality and mechanism of lingual tipping

As mentioned above, incisor lingual tipping with wear is documented in several ancient populations from north Europe and North America. Is this trait peculiar to these populations? Furthermore, has this characteristic been lost in contemporary populations?

With respect to the maxillary anterior teeth, the present study indicated that at least a slight degree of lingual tipping with wear generally occurs in every chronological Japanese sample examined (Table 3 and Figs. 3 and 4). On the other hand, there were interpopulation differences in the strength of the tendency for the maxillary anterior teeth to tip lingually. The lingual tipping was the greatest in the Jomon sample, while the Yayoi males and the Edo males showed comparatively clearer changes among the other samples. This interpopulation variation is explained by interpopulation differences in severity and pattern of tooth wear on the anterior teeth, as stated below. In the first place, this interpopulation variation is consistent with interpopulation variation in the amount of loss of mesiodistal crown dimensions accompanied with occlusal wear detected by Kaifu (1999a). In the previous study, a significant decrease in the sum of mesiodistal crown diameters from I1–M1 on one side was detected in the Jomon males and females (about 10 mm), the Yayoi males (about 3 mm), and the Edo males (about 3 mm). In addition, the present study indicated that interproximal spaces are rarely generated in the anterior segment of the adult dentitions of these samples. On the other hand, the loss of mesiodistal crown diameters was less in the maxillary dental arches of the other samples in the Yayoi and

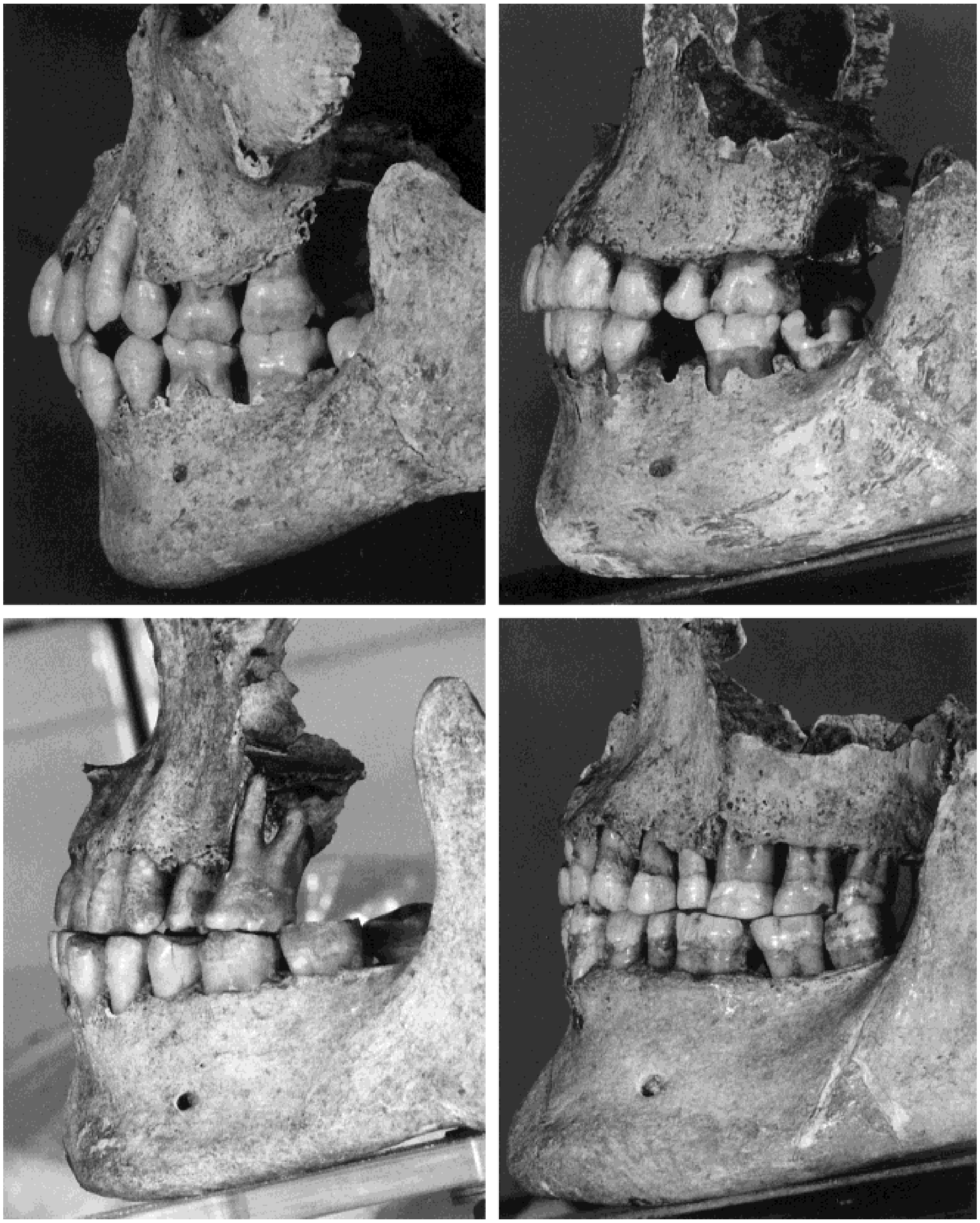

Fig. 7. A series of Jomon specimens showing changes in anterior tooth protrusion with advance of tooth wear. Dental ages of the upper two specimens are 10 (left individual) and 16 (right individual). The lower two are specimens of adult individuals. Note relationships between degree of tooth wear on the anterior teeth known from the crown height, degree of anterior tooth protrusion, overbite, and overjet. Sex of the upper left specimen is unknown because of his/her young age while the other individuals were judged as male.

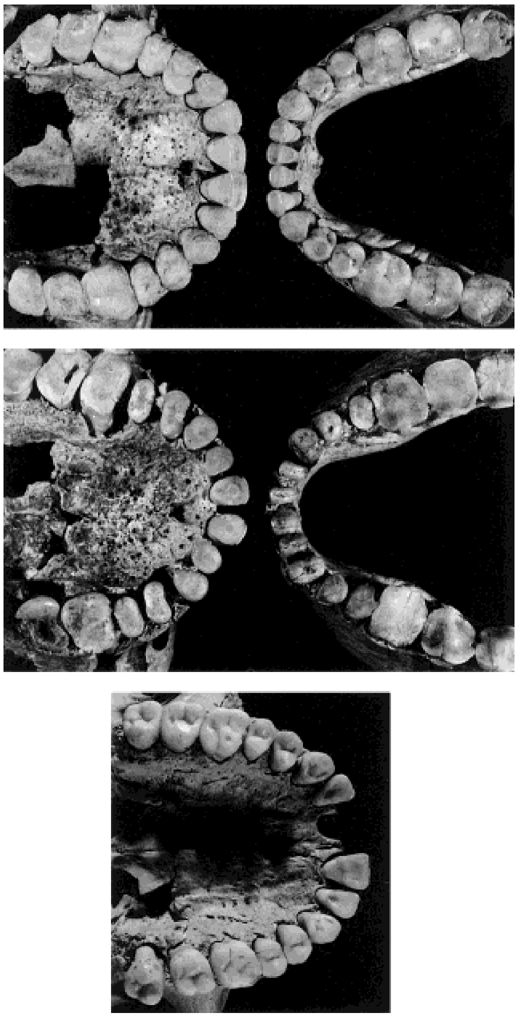

Fig. 8. Dentitions of the two Jomon (top and center) and one Kamakura (below) specimens. The Jomon specimen on the top does not exhibit interproximal spaces despite of marked tooth wear, while spaces are observed in the anterior teeth segment in the other Jomon specimen showing excessive wear. Interproximal spaces are observed in the anterior teeth segment of the maxillary dental arch of the Kamakura specimen.

later periods. Furthermore, while wear on the anterior teeth of the Yayoi males advanced to the point where *I^1 dentin thickness* reaches about 2 mm, the pattern of changes in inclination of the maxillary anterior teeth, *overbite*, and *overjet* up to this stage were basically similar to those observed in the Jomon. Tendencies seen in the other populations were also consistent with the Jomon pattern in this respect, though a limited degree of wear on the anterior teeth in these populations does not permit clear-cut comparisons.

The interpopulation variation of the inclination changes in the mandibular anterior teeth in Japan is also explained by interpopulation variation in wear severity. A remarkable lingual tipping of the mandibular anterior teeth was detected only in the Jomon and this change was not significant in the other samples. The Yayoi males and the Edo males showed comparatively marked reduction in the mesiodistal crown diameters among the samples except the Jomon (Kaifu, 1999a). However, the detected variation in the inclination changes of the mandibular anterior teeth are not unexpected because the amount of inclination change is small even in the Jomon compared to that for the maxillary antagonists. In addition, the reduction of mesiodistal crown diameters is far less in the Yayoi and Edo male samples (about 3 mm in sum from I_1–M_1 on one side) than in the Jomon (about 10 mm).

The above results are consistent with the view that remarkable changes in inclination of the anterior teeth and bite form did not occur in Japanese populations other than the Jomon because the wear on their anterior teeth did not advance to the extent necessary to cause appreciable changes. In other words, all the Japanese populations in the Yayoi and later periods probably potentially possess mechanism causing remarkable lingual tipping of the anterior teeth when severe wear occurs. The above findings also give an insight into some disagreement among the previous studies (see Background section). Some inconsistency in the behavior of the incisors seen among the previous studies may be explained by variation in the reduction of mesiodistal tooth diameters by wear. Though this possibility cannot be confirmed in many cases due to absence of published data, at least the reason why Hasund (1965) and Fishman (1976) failed to detect incisor lingual tipping in one or both arches are explained in this way if the reported values of tooth diameter reduction are compared. Thus, the balance of evidences suggests that all the living human populations potentially possess incisor lingual tipping.

Because the Jomon and Yayoi populations have different genealogical backgrounds (see Materials), it may be doubted whether the present results were sufficient to show the commonality of potential for the lingual tipping of anterior teeth among the Japanese populations. That is, although lingual tipping would occur in every Japanese chronological population if their anterior teeth were further worn, there might be interpopulation differences in the degree of its expression. However, the lingual uprighting of anterior teeth as remarkable as that seen in the Jomon was also observed in a small sample of the Okhotsk people who showed extensive tooth wear over the entire dentition (Y. Kaifu, personal observation). The Okhotsk people were inhabitants of northern Hokkaido and surrounding regions from 5th–12th centuries AD (Ishida, 1996). In a dichotomous grouping of East Asian populations such as in Turner (1987, 1990), they are grouped into the northern Asian group together with the Yayoi population (Yamaguchi, 1981), but not into the southern Asian group to which the Jomon population belongs (Turner, 1987, 1990; Matsumura, 1994).

Several factors can be postulated as possible mechanisms of lingual tipping of the anterior teeth. Tooth wear and continuous tooth eruption are two possible factors which provide room for the lingual tipping to occur. Marked lingual tipping could not occur without severe wear as indicated by differences between the Jomon and other Japanese samples in this study. However, as is suggested by the studies of Behrents (1985) and Forsberg (1979) (see above), and also by the analysis of the recent Japanese sample in the present study, a slight degree of lingual tipping may occur even in individuals with a limited degree of mesiodistal crown diameter loss in the anterior teeth by wear. In this case, the room for lingual tipping may be produced by continuous tooth eruption.

What changes of which structure causes the lingual tipping of the anterior teeth? Inclination of the tooth body accompanied by remodeling of the alveolus and retreat of the maxillary alveolar process are the two possible factors. In the former, the root form may be slightly modified by cementum deposition to the root (cf., Dean et al., 1992). The increase of the *alveolar inclination angle 1* by about 10° in the Jomon in the present study indicates that retreat of the maxillary alveolar process occurred at least to a certain degree, though a part of this change may be a result of local modification of the maxillary alveolar process tip accompanied with the remodeling of the alveolus. However, the fact that the amount of change in the *I^1 inclination angle* with wear is much greater than that in the *alveolar inclination angle 1* indicates that the changes of the tooth body is the prime mechanism in this process.

Interpretation of the initial inclinations

While it has become evident that the inclination of anterior teeth is influenced by the tooth wear pattern, interpopulation differences have been detected in initial inclination of the anterior teeth, that is, anterior tooth inclination during the formation period of the permanent dentition. In the Kamakura, Edo, and Recent samples, the inclination of the anterior teeth of subadult individuals were more variable and protrusive especially in the maxillary central incisors than in the Jomon and Yayoi. As for the maxillary canines, the Edo and Recent showed more protrusive condition than the others, including the Kamakura. Explanation of this interpopulation variation is difficult at the present stage. However, at least underdevelopment of the jaw bones may be related to the conditions seen in the Edo and Recent samples. Kaifu (1997) revealed that, through an investigation of diachronic changes in mandibular morphology based on almost the same samples as in the present study, marked reduction (overall narrowing and reduction in the regions of major masticatory muscle attachments) have occurred in Japanese mandibles from the Edo period onward. This reduction was interpreted, for several reasons, as caused mainly by underdevelopment of the jaw bone due to reduced masticatory activities. It is possible that similar reductive changes have occurred in the maxillae and this may have caused the variation seen in the initial values of the Edo and Recent samples. It is interesting in this context that the Edo and Recent populations tend to have greater

overbite and *overjet* values than the Kamakura, with some individuals showing marked deep overbite. This observation is consistent with that reported by Seguchi (1998) based on a larger sample and may also relate to the jaw reduction.

On the other hand, a similar condition of the initial values to the Edo and Recent populations was also observed in the Kamakura sample in which distinct mandibular reduction was not detected. The reason for this is difficult to explain at this stage of the research.

The present study suggested that initial inclination of the maxillary central incisors is slightly more protrusive in the Yayoi than in the Jomon samples. If this tendency seen in the small samples of the present study reflects real differences, the larger tooth dimensions in the Yayoi than in the Jomon (Brace and Nagai, 1982; Matsumura, 1994) may relate to this difference.

Interproximal spacing

Selmer-Olsen (1937) reported that while interproximal spaces were frequently observed in the permanent mandibular dentitions of adolescent Norwegian Lapps, these spaces tended to close and be crowded together with age. Mohlin et al. (1978) observed a similar age change in a sample of medieval southern Swedes. They also reported that interproximal spacing was most prevalent in the maxillary incisor segment. In contemporary populations, it is widely recognized by orthodontists that crowding frequently develops in the mandibular incisor segment during the postadolescent period (late lower arch crowding) (Richardson, 1989, 1994).

A similar tendency to that observed by Selmer-Olsen (1937) was observed in the small sample of the Jomon females of the present study. However, the conditions in the Jomon males and the Yayoi samples were not clear due to the small size of the subadult subsamples.

The Kamakura adults showed comparatively higher frequencies of interproximal spaces, especially in the maxillary arch. It seems that this condition is generated in this sample by maintaining spaces existing in the subadult period after attainment of adulthood. Although the causes of this are difficult to specify, bite form, masticatory activity, and tooth size may have played some role. While interproximal spaces are expected to occur more in individuals with smaller anterior teeth than in those with larger anterior teeth, the average tooth size is known to be smaller in the Kamakura than in the Yayoi, Edo, and Recent populations (Brace and Nagai, 1982; Matsumura, 1994). Moreover, while the Kamakura sample showed scissors bite owing to a limited degree of wear on the anterior teeth, this population is likely to have habitually engaged in strong mastication of foods compared to the Edo and later populations, as is suggested from their comparatively robust mandibles (Kaifu, 1997) and more severe tooth wear on the posterior teeth (Kaifu, 1999a). It is possible that, because of these conditions, the maxillary and mandibular anterior teeth of the Kamakura sample frequently interfered with each other in upward and downward directions, and this resulted in strong anterior tooth protrusion and maintenance of interproximal spaces in this sample. It is a well-known phenomenon in orthodontics that a patient with lost molar(s) occasionally shows strong maxillary protrusion, which is caused by occlusal interference between the maxillary and mandibular anterior teeth owing to a decreased occlusal height. It is interesting that a medieval Swedish sample examined by Mohlin et al. (1978) showed a more or less similar condition of interproximal spaces to the present Kamakura, a medieval sample from Japan.

The Edo and Recent samples were lower in observed frequencies of spaces compared to the Kamakura sample, though the frequency seems to be slightly higher in the Recent maxillae than in the Edo maxillae. This tendency is consistent with the expectation drawn from the changes in masticatory activity and resultant of mandibular reduction mentioned above. That is, it is likely that occlusal interference in the anterior dentition have been decreased and the space for the tooth row have tended to lack in these populations compared with the Kamakura condition.

An apparently odd observation was made in the study of Japanese tooth wear (Kaifu, 1999a). The amount of loss of mesiodistal crown diameters by wear was larger in the Edo males among three historic Japanese samples (the Kamakura, Edo, and Recent), whereas molar wear was shown to have been heavier in the Kamakura than in the Edo and Recent samples. The reason for this is now explained by differences in the condition of interproximal spacing. The greater loss of mesiodistal tooth diameters in the Edo males is due to more closed contact relation between the adjacent teeth compared to the Kamakura condition. Also, sex differences in the loss of mesiodistal tooth diameters in the Edo sample are explained from the observed fact that wear severity on the posterior teeth was heavier in the males than in the females (Kaifu, 1998).

CONCLUSIONS

In prehistoric Japanese populations with heavy wear over the entire dentition, the following changes were demonstrated to have occurred in the anterior segment of the dentition accompanied with wear on the anterior teeth. The anterior teeth tip lingually with wear up to a nearly upright condition to maintain contact relations between adjacent teeth of the anterior dentition by filling up interproximal spaces that would be generated by wear. The amount of lingual tipping is greater in the maxillary anterior teeth than in their mandibular antagonists, and this discrepancy is the major source of decrease of overjet and resultant attainment of edge-to-edge bite in this population. These compensatory mechanisms for wear may be potentially possessed by all living human populations independently of the degree of wear severity they suffered in their environment, though further investigation is needed to confirm this possibility.

The above findings are important support for Begg's concept of continuously changing occlusion throughout lifetime referred to in the introduction of this paper. Adult dentition and occlusion are not static as has been supposed by many dentists and anthropologists (Begg, 1954; Begg and Kesling, 1977; Brown et al., 1990). Our ancestors have long lived in environments where extensive tooth wear inevitably occurred, and it is reasonable to think that they had acquired a series of mechanisms to maintain functional occlusion against loss of tooth substances in the process of evolutionary adaptation. The lingual tipping of anterior teeth demonstrated here is interpreted as one of them. Today, the dramatic changes of the living environment caused by humans significantly reduce tooth wear on the human dentition. However, there are a number of suggestive lines of evidences that the compensatory mechanisms for heavy tooth wear are still retained in contemporary humans, indicating that we have not biologically adapted to the new environment. In this sense, the problem of occlusion should be viewed from the perspective of "Darwinian medicine" (Nesse and Williams, 1998). We should seek causative factors of a series of so-called "diseases of civilization" or "western diseases" in this sort of discrepancy between environmental changes and our adaptive status. For this purpose, it is important to investigate our original adapted status in further detail, and skeletal remains of our ancestors must have much to tell us in this respect.

ACKNOWLEDGMENTS

The author thanks Dr. Gen Suwa and Prof. Yoshiyuki Tanaka for their permission to investigate the materials in their care and Dr. Gen Suwa for invaluable suggestions. Thanks are also due to Dr. Kazutaka Adachi, Prof. Kazutaka Kasai, and Dr. Mark J. Hudson for helpful comments.

LITERATURE CITED

Anneroth G, Ericsson SG. 1967. An experimental histological study of monkey teeth without antagonist. Odont Rev 18:345–359.

Baba H, Etoh M. 1989. On the human skeletal remains of the Jomon people from eastern Japan. In: Etoh M, editor. A Study on the morphological variation of human skeletal remains of the Jomon period from eastern Japan. A Report of the Research Supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan, p 3–13 (in Japanese).

Baume LJ, Horowitz HS, Summers CJ, Backer Dirks O, Brown WAB, Carlos JP, Choen LK, Freer TJ, Harvold EP, Moorrees CFA, Salzmann JA, Schmuth G, Solow B, Taatz H. 1970. A method for measuring occlusal traits. Int Dent J 20:563–656.

Begg PR. 1954. Stone age man's dentition. Am J Orthod 40:298–312, 373–383, 462–475, 517–531.

Begg PR, Kesling PC. 1977. Begg orthodontic theory and technique. Philadelphia: W.B. Saunders.
Behrents RG. 1985. Growth in the aging craniofacial skeleton. In: Carlson DS, Ribbens KA, editors. Monograph 7. Craniofacial growth series. Ann Arbor: University of Michigan, Center for Human Growth and Development.
Berry DC, Poole DFG. 1974. Masticatory function and oral rehabilitation. J Oral Rehabil 1:191–205.
Berry DC, Poole DFG. 1976. Attrition: possible mechanisms of compensation. J Oral Rehabil 3:201–206.
Björk A, Palling M. 1955. Adolescent age changes in sagittal jaw relation, alveolar prognathy, and incisal inclination. Acta Odont Scand 12:201–232.
Brace CL. 1977. Occlusion to the anthropological eye. In: McNamara J, editor. The biology of occlusal development. Ann Arbor, MI: Center for Human Growth and Development. p 179–209.
Brace CL, Mahler PE. 1971. Post-Pleistocene changes in human dentition. Am J Phys Anthropol 34:191–204.
Brace CL, Nagai M. 1982. Japanese tooth size: Past and present. Am J Phys Anthropol 59:399–411.
Brown T, Townsend GC, Richards LC, Burgess VB. 1990. Concept of occlusion: Australian evidence. Am J Phys Anthropol 82:247–256.
Campbell TD. 1925. Dentition and palate of the Australian Aborigine. Adelaide: The Hassell Press.
Clarke NG, Hirsch RS. 1991a. Physiological, pulpal, and periodontal factors influencing alveolar bone. In: Kelley MA, Larsen CS, editors. Advances in dental anthropology. New York: Wiley-Liss, Inc. p 241–266.
Clarke NG, Hirsch RS. 1991b. Tooth dislocation: The relationship with tooth wear and dental abscesses. Am J Phys Anthropol 85:293–298.
Cohen MN. 1989. Health and the rise of civilization. New Haven, CT: Yale University Press.
Cohen MN, Armelagos GJ. 1984. Paleopathology at the origin of agriculture. New York: Academic Press.
Compagnon D, Wada A. 1991. Supraeruption of the unopposed maxillary first molar. J Prosthet Dent 66:29–34.
Corruccini RS. 1990. Australian aboriginal tooth succession, interproximal attrition, and Begg's theory. Am J Orthod Dentofac Orthop 97:349–357.
Corruccini RS. 1991. Anthropological aspects of orofacial and occlusal variations and anomalies. In: Kelley MA, Larsen CS, editors. Advances in dental anthropology. New York: Wiley-Liss. p 295–323.
D'Amico A. 1958. The canine teeth—normal functional relation of the natural teeth of man. J South Calif Dent Assoc 26:6–23, 49–60, 127–142, 175–182, 194–208, 239–241.
D'Amico A. 1961. Functional occlusion of the natural teeth of man. J Prosthet Dent 11:899–915.
Dean MC, Jones ME, Pilley JR. 1992. The natural history of tooth wear, continuous eruption and periodontal disease in wild shot great apes. J Hum Evol 22:23–39.
Dickson GC. 1979. Concepts of occlusion. Ann Roy Coll Surg Engl 61:177–182.
Emslie RD. 1952. The ideal occlusion for periodontal health. Dent Rec 72:179–188.
Fishman LS. 1976. Dental and skeletal relationships to attritional occlusion. Angle Orthod 45:61–63.
Forsberg CM. 1979. Facial morphology and ageing: a longitudinal cephalometric investigation of young adults. Eur J Orthod 1:15–23.
Greenfield LO. 1977. *Ramapithecus* and early hominid origins. Ph.D. Dissertation, University of Michigan.
Hasund AP. 1965. Attrition and dental arch space. Trans Eur Orthod Soc:121–131.
Hudson MJ. 1999. Ruins of identity: ethnogenesis in the Japanese islands. Honolulu: University of Hawaii Press.
Humerfelt A, Slagsvold AO. 1972. Changes in occlusion and craniofacial pattern between 11 and 25 years of age. Trans Eur Orthod Soc:113–122.
Hunt EE. 1961. Malocclusion and civilization. Am J Orthod 47:406–422.
Hylander WL. 1977. Morphological changes in human teeth and jaws in a high-attrition environment. In: Dahlberg AA, Graber TM, editors. Orofacial growth and development. Paris: Mouton Publishers. p 301–333.
Ishida H. 1996. Metric and nonmetric cranial variation of the prehistoric Okhotsk people. Anthropol Sci 104: 233–258.
Johansson A, Kiliaridis S, Haraldson T, Omar R, Carlsson GE. 1993. Covariation of some factors associated with occlusal tooth wear in a selected high-wear sample. Scand J Dent Res 101:398–406.
Kaifu Y. 1996. Edge-to-edge bite and tooth wear. Bull Natn Sci Mus, Tokyo, Ser D 22:45–54.
Kaifu Y. 1997. Changes in mandibular morphology from the Jomon to modern periods in eastern Japan. Am J Phys Anthropol 104:227–243.
Kaifu Y. 1998. Sex differences in tooth wear in Japan. Bull Natn Sci Mus, Tokyo, Ser D 24:49–59.
Kaifu Y. 1999a. Changes in the pattern of tooth wear from prehistoric to recent periods in Japan. Am J Phys Anthropol 109:485–499.
Kaifu Y. 1999b. Changes in alveolar prognathism and anterior teeth protrusion in Japan. Anthropol Sci 107:3–24.
Kirveskari P. 1979. Cusps or no cusps—that is not the question. J Oral Rehabil 6:311–316.
Krogstad O, Dahl BL. 1985. Dento-facial morphology in patients with advanced attrition. Eur J Orthod 7: 57–62.
Larsen CS. 1997. Bioarchaeology: Interpretating behavior from the human skeleton. Cambridge: Cambridge University Press.
Leigh AB. 1929. Dental pathology of aboriginal California. Dental Cosmos 71:756–767.
Love RJ, Murray JM, Mamandras AM. 1990. Facial growth in males 16 to 20 years of age. Am J Orthod Dentofac Orthop 97:200–206.
Luke DA, Lucas PW. 1983. The significance of cusps. J Oral Rehabil 10:197–206.
Lundström A, Lysell L. 1953. An anthropological examination of a group of medieval Danish skulls, with particular regard to the jaws and occlusal conditions. Acta Odont Scand 11:111–128.
Lysell L. 1958. Qualitative and quantitative determination of attrition and the ensuing tooth migration. Acta Odont Scand 16:267–292.
Lysell L, Filipsson R. 1958. A profile roentgenologic study of a series of medieval skulls from northern Sweden. Odontol Tidskrift 66:161–174.
Matsumura H. 1994. A microevolutional history of the Japanese people from a dental characteristics perspective. Anthropol Sci 102:93–118.
Mikami T. 1956. On the age of the human skeletons from the Zaimokuza site in Kamakura. In: Medieval Japanese skeletons from the burial site at Zaimokuza, Kamakura City. Tokyo: Iwanami-shoten. p 67–74 (in Japanese with English summary).
Mohlin B, Sagne S, Thilander B. 1978. The frequency of malocclusion and the craniofacial morphology in a medieval population in southern Sweden. OSSA 5: 57–84.
Moorrees CFA. 1957. The Aleut dentition: A correlative study of dental characteristics in an Eskimoid people. Cambridge, MA: Harvard University Press.

Murphy T. 1958. Mandibular adjustment to functional tooth attrition. Aust Dent J 3:171–178.
Murphy T. 1959. Compensatory mechanisms in facial height adjustment to functional tooth attrition. Aust Dent J 4:312–323.
Nakahashi T. 1993. Temporal craniometric changes from the Jomon to Modern period in western Japan. Am J Phys Anthropol 90:409–425.
Nesse RM, Williams GC. 1998. Evolution and origins of disease. Sci Am November: 58–65.
Owen CP. 1986. The prophyletic reduction of cusps—is it desirable? J Oral Rehabil 13:39–48.
Perera PSG. 1987. Rotational growth and incisor compensation. Angle Orthodont 57:39–49.
Reinhardt GA. 1983a. Attrition and edge-to-edge bite: An anthropological study. Angle Orthod 53:157–164.
Reinhardt GA. 1983b. Relationships between attrition and lingual tilting in human teeth. Am J Phys Anthropol 61:227–237.
Richardson ME. 1989. The role of the third molar in the cause of late lower arch crowding: A review. Am J Orthod Dentofac Orthop 95:79–83.
Richardson ME. 1994. The etiology of late lower arch crowding alternative to mesially directed forces: A review. Am J Orthod Dentofac Orthop 105:592–597.
Sarnäs KV, Solow B. 1980. Early adult changes in the skeletal and soft-tissue profile. Eur J Orthod 2:1–12.
Seguchi N. 1998. Secular change of Japanese occlusion: The frequency of the overbite and its association with food preparation techniques and eating habits. Am J Phys Anthropol Suppl. 26:199 (abstract).
Selmer-Olsen R. 1937. The normal movement of the mandibular teeth and the crowding of the incisors as a result of growth and function. Eur Orthod Soc Report of 21st Annual Congress. p 136–148.
Siatkowski RE. 1974. Incisor uprighting: Mechanism for late secondary crowding in the anterior segments of the dental arches. Am J Orthod 66:398–410.
Smith KC. 1934. Some notes on the dentitions of Anglo-Saxon skulls from Bidford-on-Avon, with special reference to malocclusion. Dent Rec 54:1–21.
Turner CG II. 1987. Late Pleistocene and Holocene population history of East Asia based on dental variation. Am J Phys Anthropol 73:305–321.
Turner CG II. 1990. Major features of sundadonty and sinodonty, including suggestions about east Asian microevolution, population history, and Late Pleistocene relationships with Australian Aboriginals. Am J Phys Anthropol 82:295–317.
Ubelaker DH. 1989. Human skeletal remains, 2nd ed. Washington, DC: Taraxacum.
Ungar PS, Fennel KJ, Gordon K, Trinkaus E. 1997. Neandertal incisor beveling. J Hum Evol 32:407–421.
Ungar PS, Grine FE. 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. J Hum Evol 20:313–340.
Varrela J. 1990. Effects of attritive diet on craniofacial morphology: a cephalometric analysis of a Finnish skull sample. Eur J Orthod 12:219–223.
Walker PL. 1973. Great ape feeding behavior and incisor morphology. Ph.D. dissertation, University of Chicago.
Yamaguchi B. 1981. 7. Ancient human skeletal remains from Hokkaido. In: Ogata T, editor. The Japanese I. Yuzankaku-shuppan. p 137–156 (in Japanese).